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REVIEW OF VON GUAITA'S EXPERIMENTS IN BREEDING MICE.

C. B. DAVENPORT.

In the two latest volumes of the Berichte der Naturforschenden Gesellschaft zu Freiburg, G. von Guaita gives the results of his breeding experiments. He started in 1896 with fifty-five Japanese walzing mice and with numerous white mice belonging to a race bred by Weismann since 1888, and made crossings through seven generations to 1900. His main data concern the inheritance of color; incidentally, data were got on the diminution of fertility with in-and-in breeding.

Diminution of Fertility.

These results were gained chiefly from Weismann's breedings. The total number of young, the number of litters, and the number of young per litter are given below for each decade of generations.

1st to 10th gen	eration :	1345	young;	219	litters;	avg.	young	per	litter,	6. ı	
11th to 20th	"	352	"	62	"	"	"	"	"	5.6	
21st to 29th	"	124	"	29	"	"	"	"	"	4.2	

In von Guaita's breedings:

1st and 2d ger	nerations,		•	"	"	"	"	3.5
3rd and 4th	"			"	"	"	"	3.7
5th and 6th	"			"	"	"	"	2.0

Thus in the successive generations there is a reduction in fertility of about thirty per cent; and this is probably due to too close breeding.

Color of Mixtures.

Japanese walzing mice vary in color, but are chiefly piebald — black and white. White mice are without pigment (true albinos) and breed very true.

Crosses of walzing $\mathfrak{P} \times$ white \mathfrak{F} and white $\mathfrak{P} \times$ walzing \mathfrak{F} gave twenty-eight young. All were of a gray color and indistinguishable either in respect to color or size from the common house mouse. Also in temperament they were like the house mouse, for they were very wild and lively (unlike either parent) and the walzing action was entirely absent from all the mice of this second generation. Similar results were got by Haacke (95) after crossing the same races. Haacke says: "When you pair a blue and white spotted walzing mouse with a common white mouse you get either (and usually) uniformly gray mice, which cannot be distinguished from the wild house mouse, or else (more rarely) uniformly black mice." These results, then, lead to the conclusion that when very unlike races of mice are crossed the result is often or usually a reversion.

A third generation was next produced by von Guaita by mating two of the gray mice or reversions. Four pairs were thus mated and forty-four young were reared—all having both parents gray, and half their grandparents walzing and half white. These fourty-four mice are placed in nine color classes, as follows:

				Per cent
"House"	entirely gray,	•	15	
	gray with isolated markings,		7 } 25	57
type.	black [essentially house type],		3	
Albino.	pure white, red eyes,		11	25
(white walzers,		3)	
117 - 7 - 2	gray-white spotted walzers, .		I	
Walzing type.	gray walzers,	•	2 } 8	18
type.	black-white spotted walzers, .		1	
į	black walzers,	•	ı	
			44	100

The most striking phenomenon of this third generation is the sudden occurrence of great variation. In the language of plant breeders "the *type* is broken." Plant breeders (*e.g.*, Focke and de Vries) have long ago observed that the progeny of hybrids is extraordinarily variable.

Fourth Generation. — Several pairs of the foregoing descendants of the reverted gray mice were mated, and thirty-one young sorted into eight classes were obtained, as follows:

Third Generation	Gray Q White- Walzer &	Gray Q White 3	White Q White 3	Gray and Spotted Q Gray and Spotted 3	Total	Sum	Per Cent
Uniformly gray	2	12			14		
Gray with markings		2		2	4	İ	
Black	2				2	20	65
Albinos	I		4			5	16
Uniformly gray walzers	I	I			2		
Gray walzers with spots		I	ì		I		
Black-white walzers	1				I		
Black walzers	2				2	6	19
	9	16	4	2		31	100

As in the third generation, there is here great variation. The results may be generalized as follows:

- (1) All descendants of albinic parents are albinos.
- (2) When both parents are gray and spotted all descendants (2) are gray and spotted.
- (3) Gray \mathcal{P} × white \mathcal{F} gives 88 per cent gray and 12 per cent walzers; the white is shut out.
- (4) Gray $9 \times \text{ white walzer } 3 \text{ gives } 44 \text{ per cent gray, } 44 \text{ per cent walzers, and } 12 \text{ per cent white.}$

Fifth Generation. — To save room we will henceforth make use of abbreviations for the names of colors, as follows:

G = gray.

Gw = gray with white markings.

B = uniformly black.

Bw = black with white markings.

A = albino or white.

Ww = white walzers.

Wg = gray walzers.

Wgw = gray-white walzers.

Wb = black walzers.

Wbw = black and white walzers.

The female parent invariably precedes the male.

Sum Cent		-	82 73	91 81					13 11	113 100
Total	- 5	6	19		-	63	8	3	S	
6 4 Gw Gw × Gw	91									91
$(G \times A) \times (Gw \times Gw)$ $Gw \times Gw$	35)		6						44
$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$	6	ı	7				8			13
3 $(G\times W_w)\times (G\times A)$ $B_w\times W_g$	H			H		H				3
2 ×(GQ×Ww3) BwQ×B3		∞	01	7				8	Ŋ	32
1 (GQ×Ww\$)> WbQ×B&			87	-	н			H		5
Gen. III IV	ს ჭ	В	Bw	₹	WW	Wg	Wgw	Wb	Wbw	

Gen.		C			Total	Sum	Per Cent	
II								
ш	A, 2; Gw, 4; G, 2 Gw, 4	{ A, 1; Gw, 2; } G, 3; Ww, 2 }	Gw, 2; G,	3; Ww, 3	G, 4; Ww, 4			
ıv	Gw, 4	{ Gw,1; Bw,1; } { Wg,1; Wb,1 }	{ Gw, 1; B, 1;	Bw, 1;}	Bw,1; B,2; W,1			
V	Gw x Gw	Wgw × G	B×A	Wb × B	A × Ww			
G	I	I				2		
Gw	20	I				21		
В			7	I		8		
$\mathbf{B}\mathbf{w}$			16	I		17	48	58
A	10		18		4		32	38
Ww			2			2		
Wb	,	I				I	3	4
	31	3	43	2	4		83	100

Sixth Generation.

Seventh Generation. — The colors of only eight members of this generation were determined — too few to be significant.

General Results.

In the successive generations the percentage of walzing individuals undergoes a steady decline from eighteen per cent and nineteen per cent in the third and fourth generations to eleven per cent in the fifth and four per cent in the sixth generation. Is this decline due to the elimination of an unstable condition or to the circumstance that too little of the walzing blood has been employed in the later crosses to keep up the original proportion? The question whether the normal law of inheritance is followed here may, indeed, be asked of all the colors. The normal law of inheritance, as defined by Galton, is that one-half the heritage of any generation is derived from the parents, one-fourth from the grandparents, one-eighth from the great-grandparents, and so on, according to the formula:

Inheritance = $\frac{1}{2} k_1 + \frac{1}{4} k_2 + \frac{1}{8} k_3 + \frac{1}{16} k_4 + \text{etc.}$

To apply the normal law of inheritance it is convenient to assume it and to compare the theoretical heritage with the empirical. If the two agree, the validity of the law is established in this case; conversely, if the two do not agree, the law does not hold. This method of testing the law is the same as that employed by Galton ('98) in the case of Bassett hounds. It may be illustrated by the calculation of the theoretical number of albinos in the sixth generation. Let us take the first column. If one of the two parents were an albino, we should expect at least $\frac{1}{2} \times 50\%$ of the progeny to be such. If both parents were A, $\frac{2}{2} \times 50\%$ of progeny at least should be A. If, in addition, all of the grandparents (Gen. IV) were A, we should expect at least $\frac{2}{3} \times 50\% + \frac{4}{4} \times 25\%$ of the VI Gen. to In general, if n_{v} , n_{iv} , n_{iii} , etc., represent the number of times an albino appears as ancestor in the different generations, then the proportion of albinos in the sixth generation should be:

$$\%A_{vi} = \frac{n_{v}}{2} \times 50\% + \frac{n_{iv}}{4} \times 25\% + \frac{n_{iii}}{8} \times 12.5\% + \frac{n_{ii}}{16} \times 6.25\% + \frac{n_{i}}{32} \times 3.125\% + \frac{1}{2} \times 3.125\%.$$

The last term is got by observing that the ancestors of half of the first generation were exclusively albinos for many generations, while the ancestors of the other half were exclusively walzers. The value of A is similarly calculated for each column, and the theoretical number of individuals for each column is found. Their sum should be equal to the observed number, or, when reduced to percentages, to the observed percentage of total. The closeness of theory to observation is sometimes striking. Thus if we compare column by column the observed and theoretical frequencies of walzers in the fifth generation we get:

In the following table are given for each generation the observed and (in parenthesis) the corresponding calculated percentages for each color:

GENERATION	I	II	III	IV	v	VI
Black alone (B) {)	o (o)	7 (o)	7 (o)	25 (18)	30 (40)
Gray less black (G) {	o 	(o)	50 (50)	58 (48)	48 (60)	28 (28)
Total gray and black	0	100	57 (50)	65 (48)	73 (78)	58 (69)
Albinos \ldots $\left\{ \begin{array}{lll} 5 \end{array} \right.$	0	o (50)	25 (25)	16 (32)	16 (9)	38 (18)
Walzers \dots $\left\{ 5 \right\}$	0	o (50)	18 (25)	19 (20)	11 (13)	4 (13)

Several remarkable things come out of this table. In the first place the most marked departure from Galton's Law of Ancestral Inheritance is seen in the second generation, where the gray, non-walzing reversions suddenly made their appearance. We know as yet little concerning the laws of the phenomenon called "reversion"; but whether it be considered a remote atavism or only an apparent "inheritance," it seems equally to form an exception to Galton's Law.

Secondly, the case of the walzers does indeed look like an exception to Galton's Law. It looks as though the walzing condition were an unstable condition being rapidly eliminated. In so far the result opposes the usual expectation of sport prepotency.

Thirdly, the albinos, likewise sports, apparently are prepotent, since there is twice the proportion there should be in the sixth generation. The numbers are so large that one can hardly object that these figures are not altogether significant.

Fourthly, the grays run close to theory, excepting always generation II. They are nearest to the original type of *Mus musculus* and seem to inherit in the most nearly normal fashion.

In conclusion, then, we may say that the data afforded by these breeding experiments indicate, so far as they go, that Galton's Law of Inheritance holds only with form units which are not very divergent from the type, and that among sports we may have some that show a great stability and prepotency, while we may occasionally have others which are physiologically so unfit that they are unstable and have less than normal potency.

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